

Architectonica (Architectonica) karsteni (Rutsch, 1934):
A Neogene and Recent Offshore Contemporary of
A. (Architectonica) nobilis Röding, 1798
(Gastropoda: Mesogastropoda)

by

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Abstract. The subdued spiral and axial sculpture of the Miocene-early Pliocene mesogastropod *Architectonica (Architectonica) nobilis karsteni* Rutsch, 1934, has been used to distinguish it from the more granulose *A. (Architectonica) nobilis nobilis* Röding, 1798, a long-ranging and widespread species of the Caribbean and western tropical American shelf. Especially noteworthy in the former taxon is the absence ventrally of a second, noded spiral cord and a second, wide spiral groove. Discovery of Plio-Pleistocene specimens in northwestern Peru and Recent specimens from western tropical America, all referable to *A. nobilis karsteni*, suggests that this form has maintained its phenotypic, and presumably genotypic, integrity for as long as *A. nobilis nobilis*. A re-analysis of the shell morphology of *A. nobilis karsteni* and a fresh consideration of its habitat suggest that the subspecies should be accorded specific rank, namely, *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

INTRODUCTION

Architectonica (Architectonica) nobilis nobilis Röding, 1798, is a low-spiral, solidly built mesogastropod characterized by its granulose texture and strong spiral sculpture. This species is a common constituent of Neogene and Recent shelf faunas of the Caribbean and eastern tropical Pacific Ocean (WOODRING, 1959; KEEN, 1971; ABBOTT, 1974). *Architectonica nobilis karsteni* Rutsch, 1934, is smoother and less sculptured than the type form. It is also less common, heretofore reported only from early Miocene to early Pliocene sedimentary rocks of the southern Caribbean, Mexico, and Chile (e.g., BOSE, 1906; JUNG, 1965; FRASSINETTI & COVACEVICH, 1981; see Figure 1). This paper reports the first discovery of *A. nobilis karsteni* from Plio-Pleistocene sediments and in modern shelf environments of western tropical America.

In 1981 and 1982 the author found several partial molds of the "karsteni" form in gravelly-shelly sandstones near the base of the Mancora Tablazo sequence in northwestern Peru and in overlying siltstones of the same sequence

(Figure 1). These deposits were first described in some detail by BOSWORTH (1922), and lately have been re-examined by DEVRIES (1982, and in preparation), the latter author attributing the coarse and fine sediments, respectively, to semi-protected inlet and deep lagoonal environments.

Numerous specimens of *Architectonica nobilis karsteni* were recently recognized by the author among the collections of *A. nobilis nobilis* housed at the Los Angeles County Museum of Natural History (LACM). This material was collected live from midshelf depths between Baja California and Ecuador by the R/V *Anton Bruun* and other vessels (Figure 1). A consideration of the taxonomy of these specimens of *A. nobilis karsteni* is presented below, followed by a discussion of the ecological data available for fossil and modern occurrences. It will be argued that the longevity of the "karsteni" form, its morphological and ecological integrity, and possible European ancestry, together suggest the propriety of full specific rank for this taxon, herein identified as *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

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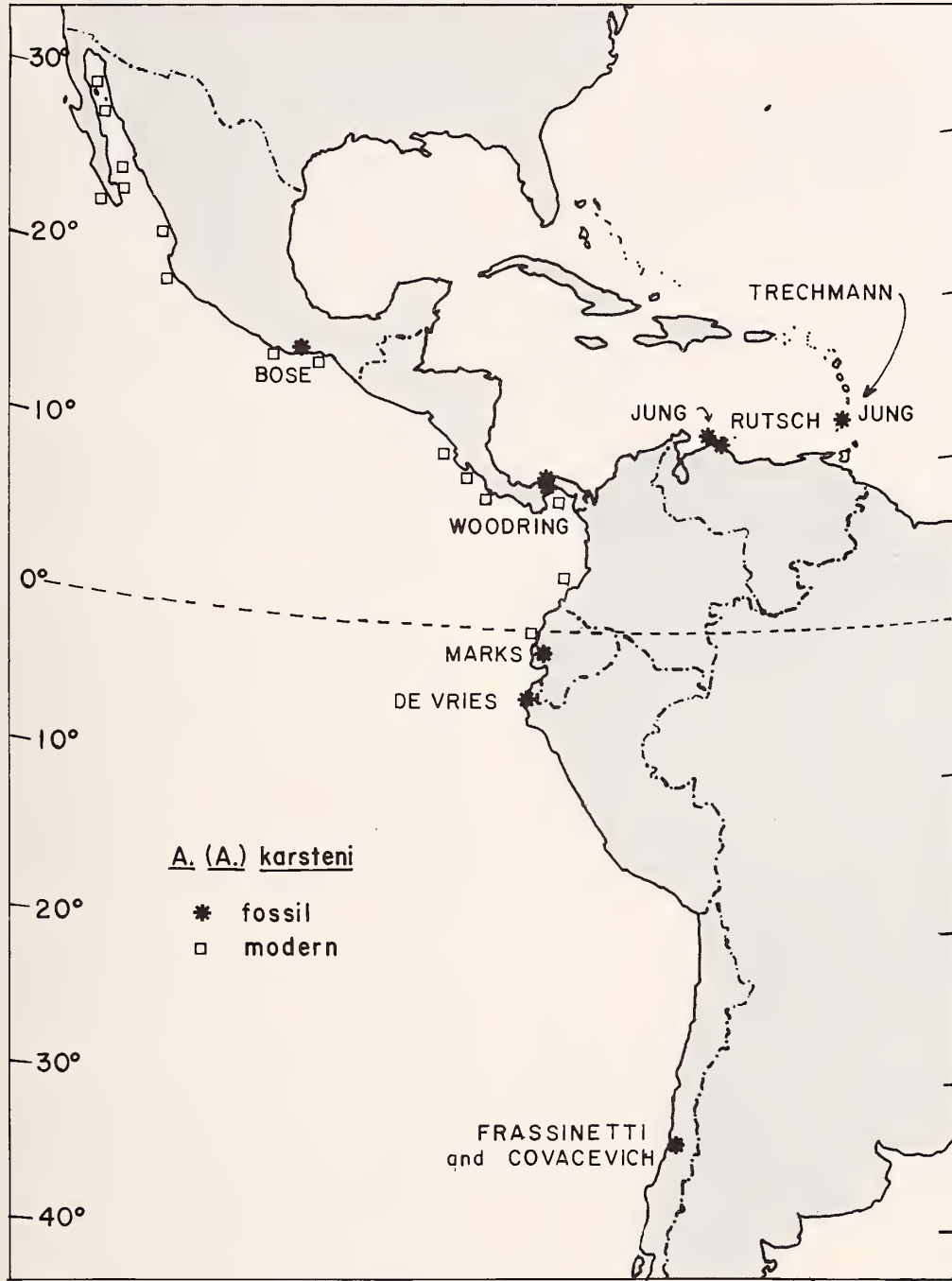


Figure 1

Neogene and Recent distribution of *Architectonica* (*Architectonica*) *karsteni* (Rutsch). Each fossil locality is designated by the author of the record.

TAXONOMY

Class Gastropoda

Subclass Prosobranchia

Order Mesogastropoda

Superfamily Architectonicacea

Family Architectonicidae Gray, 1850

Subfamily Architectonicinae Gray, 1850

Diagnosis: "Mainly heavy and solid species, 30–70 mm max. diam., a few as small as 7.5 mm. Single peripheral keel. Sculpture of strong cords and grooves, granose, tessellated or almost smooth. Umbilicus wide and perspective to narrow. Operculum chitinous, thin and flat" (GARRARD, 1977:510).

Genus *Architectonica* Röding, 1798Subgenus *Architectonica* Röding, 1798

Type species: By subsequent designation (GRAY, 1847:151), *Trochus perspectivus* Linné, 1758.

Diagnosis: "Large to very large, medium to low conical; medium to wide perspective umbilicus; strong peripheral keel separated by a deep groove from both a dorsal and basal cingulum; usually both axially and spirally grooved and beaded, especially in early whorls; flat horny operculum . . ." (GARRARD, 1977:510).

Architectonica (*Architectonica*) *karsteni*
(Rutsch, 1934)

Figures 2–12, 15, 16, 18, 20

Architectonica nobilis karsteni RUTSCH, 1934:44, pl. 1, figs. 8–10.

Architectonica sexlinearis haughti MARKS, 1951:93, pl. 2, figs. 2, 6.

Architectonica (*Architectonica*) *nobilis karsteni* Rutsch, 1934. WOODRING, 1959:167–168, pl. 30, figs. 1–3; JUNG, 1965:488–489, pl. 64, figs. 8–10; JUNG, 1971:177, pl. 6, figs. 5, 6; FRASSINETTI & COVACEVICH, 1981:149–152, figs. 2a–2c.

Architectonica (*Architectonica*) *nobilis* subsp. WOODRING, 1973:473, pl. 71, figs. 4, 5, 10, 11.

Solarium gatunense TOULA, 1908. TRECHMANN, 1935:549, pl. 21, figs. 21, 22.

[non] *Solarium gatunense* TOULA, 1908:692–693, pl. 25, fig. 3 (= *Architectonica nobilis* Röding, 1798).

Solarium villareloi BOSE, 1906 (in part):30–31, pl. 3, figs. 6, 7.

Original description: Shell rather low-spined; base strongly convex; umbilicus narrow. Base ornamented completely differently than *Architectonica nobilis*: on the keel, which surrounds the umbilicus, a deep wide furrow follows outward and after that a wide zone with strong radial folds. The two (up to three) granular spiral cords that characterize *A. nobilis* are missing. Before the periph-

eral keel lies a partly granular spiral cord. The strong spiral thread that lies between both of these cords of the type specimen of *A. nobilis* is also missing . . . (free translation from original German description of RUTSCH, 1934).

Type locality: Punta Gavilan, northern Venezuela ("Cantaure" Formation, Miocene; RUTSCH, 1934).

Location of type: Museum of Basel, Holotype 142/1769, Museum No. 13.

Additional material: LACM 66-198. Four specimens from R/V *Anton Bruun* cruise 18B, Station 778, 93 m, W of Cabo Pasado, Ecuador (00°21'S, 80°41'W) collected live. LACM collections contain other specimens of *A. karsteni* whose distributions are illustrated in Figures 1 and 22.

OSU 36792. External mold of umbilical region and portions of base. Detail is well-preserved in calcareous gravelly sand. Collected by T. DeVries in 1981 from near base of Mancora Tablazo section at Cabo Blanco, northwest Peru.

Supplementary description: LACM 66-198a, b, c, d. Small to moderate size (see Table 1), only moderately thick, conical; umbilical width about $\frac{2}{3}$ total diameter. Protoconch not visible; telococonch with 7 whorls. Dorsal sculpture one narrow, flattened, peripheral cord and four wider cords, all granulose in early whorls, becoming smooth or nearly smooth on body whorl; cords bear minute spiral striae and on the two abaxial dorsal cords, a single weak spiral groove; grooves between dorsal cords narrow, usually $\frac{1}{5}$ to $\frac{1}{6}$ as wide as adjoining cords. Ventral sculpture consists of umbilical cord with numerous blunt rectangular nodes; adjoined peripherally by wide, deep, flat-bottomed groove. A sharply rounded spiral cord and spiral thread lie adjacent to peripheral dorsal cord. Intervening ventral area convex, crossed by radially splayed wrinkles that gradually fade peripherally; wrinkles intersected by 6 weakly developed spiral grooves and numerous minute spiral striae. Weak parietal groove emerges on columellar lip $\frac{1}{3}$ the distance abapically from the edge of succeeding whorl to the siphonal canal; a second weaker groove is present anteriorly. Color uniformly pale brown with radially directed bands of rectangular brown spots on dorsal cords and discontinuous thin spiral bands of brown on ventral side. Thin brown periostracum. Flat, chitinous operculum.

OSU 36792. Moderate size (27 mm diameter); umbilical cord with large rectangular nodes; bound peripherally by a single wide, deep, flat-bottomed spiral groove. Radially splayed, well-defined wrinkles, fading peripherally; single spiral cord against peripheral cord without intervening spiral thread. Ventral area with 4, possibly 6, weak spiral grooves passing between wrinkles.

Stratigraphic and geographic distribution: Northern Venezuela, middle Miocene (RUTSCH, 1934; JUNG, 1965); Carriacou (eastern Caribbean), late early–middle Mio-

cene (TRECHMANN, 1935; JUNG, 1971); Panama, early Miocene–early Pliocene (WOODRING, 1959, 1973); northern Colombia, Miocene (J. W. Durham, personal communication, 1984); Ecuador, middle Miocene (MARKS, 1951), upper Miocene (Olsson, unpublished USNM material, USGS Locality 23491); central Chile, early–middle Miocene (FRASSINETTI & COVACEVICH, 1981); southeastern Mexico, (?) early Pliocene (BOSE, 1906; J. W. Durham, personal communication, 1984); northwestern Peru, late Pliocene–early Pleistocene; Gulf of California to Ecuador, Recent (Figure 1, Table 2).

DISCUSSION

Although similar, *Architectonica karsteni* and *A. nobilis* may be distinguished by several important morphologic features, the most obvious being the absence ventrally of both a second strongly noded spiral cord and a second deep spiral groove on *A. karsteni* (see FRASSINETTI & COVACEVICH, 1981). Other spiral grooves do appear on the ventral face of *A. karsteni*, but these in no way resemble the deep grooves of either species (see Figures 5, 13). The latter are wide and squarely cut with a flat bottom. The former are usually narrow, shallow, and V-shaped. Significant gradations between these two groove forms are rarely seen in the Recent material from LACM collections and apparently never found in fossil specimens.

Most specimens of Recent *Architectonica karsteni* are thinner-shelled, lower-spired, more convexly rounded dorsally and ventrally, less granulose, and more uniformly colored in drab brown than *A. nobilis*. Dorsally, spiral grooves are narrower in *A. karsteni*; in *A. nobilis*, any of

the dorsal grooves may be nearly half as wide as the adjacent cords.

The spiral thread situated between the dorsal peripheral cord and the ventral cord near the periphery is present to some degree in all Recent specimens of *Architectonica karsteni*, as are all four dorsal grooves. In these two respects they resemble *A. nobilis* more than fossil *A. karsteni*, which usually lack the spiral thread and one or two of the dorsal grooves.

The columellar lip of all *Architectonica karsteni* is quite different from that of *A. nobilis*. The latter has a well-developed groove only one-fourth to one-fifth the columellar lip length below the superseding whorl, rather than one-third as in *A. karsteni* (Figures 16, 18–21). Anteriorly, the columellar lip of *A. nobilis* bears several tiny pleats and grooves that are not present in *A. karsteni*.

Specimens of *Architectonica karsteni* from Panama (WOODRING, 1959) and Ecuador (MARKS, 1951) were examined and compared with the newly discovered specimens (Table 1). Dorsally, fossils from both localities were somewhat less granulose and lacked one of four dorsal grooves. Ventrally, the Panama specimens (USNM 562636) lacked the incipient spiral grooves present across the entire base of the Recent specimens, but in the Ecuadorian specimens these nascent grooves (four in number) were readily visible. Undescribed upper Miocene *A. karsteni* from Ecuador collected by Olsson and housed at the U.S. National Museum (USGS Locality 23491) even display a third, thin spiral thread near the periphery as is seen on Recent specimens.

A close examination of the figure of *Solarium gatunense* TOULA (1908) reveals two deep grooves encircling the um-

Explanation of Figures 2 to 14

Figures 2 to 12. *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

Figure 2. LACM 66-198d. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. ($\times 1.67$).

Figure 3. LACM 66-198b. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. ($\times 1.67$).

Figure 4. LACM 66-198c. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. ($\times 1.67$).

Figure 5. LACM 66-198d. Ventral view. ($\times 1.67$).

Figure 6. LACM 66-198b. Ventral view. ($\times 1.67$).

Figure 7. LACM 66-198c. Ventral view. ($\times 1.67$).

Figure 8. LACM 66-198d. Apertural view. ($\times 1.67$).

Figure 9. LACM 66-198b. Apertural view. ($\times 1.67$).

Figure 10. LACM 66-198c. Apertural view. ($\times 1.67$).

Figure 11. OSU 36792. Late Pliocene–early Pleistocene, base of Mancora Tablazo sequence, Cabo Blanco, Peru. Latex cast of partially preserved ventral surface and umbilicus. ($\times 1.4$).

Figure 12. OSU 36792. Original sandstone mold from which latex cast (Figure 11) was made. ($\times 1.4$).

Figures 13 and 14. *Architectonica (Architectonica) nobilis* Röding, 1798.

Figure 13. LACM AHF-93839. Recent, Costa Rica. Ventral view showing two deep spiral grooves encircling umbilicus. ($\times 1.81$).

Figure 14. LACM AHF-93839. Dorsal view showing wide dorsal spiral grooves. ($\times 1.81$).



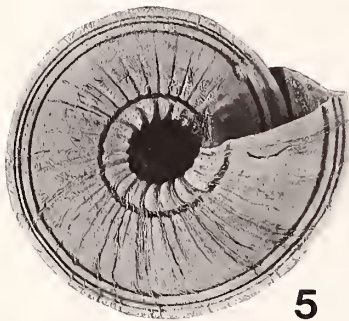
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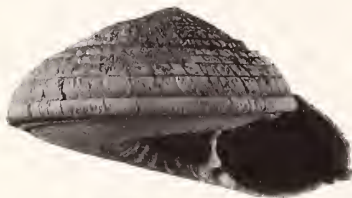
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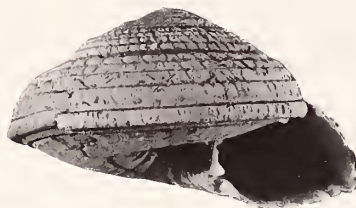
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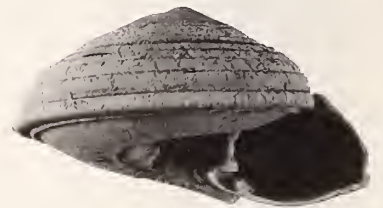
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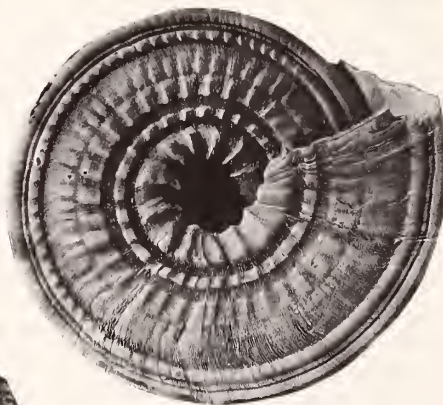
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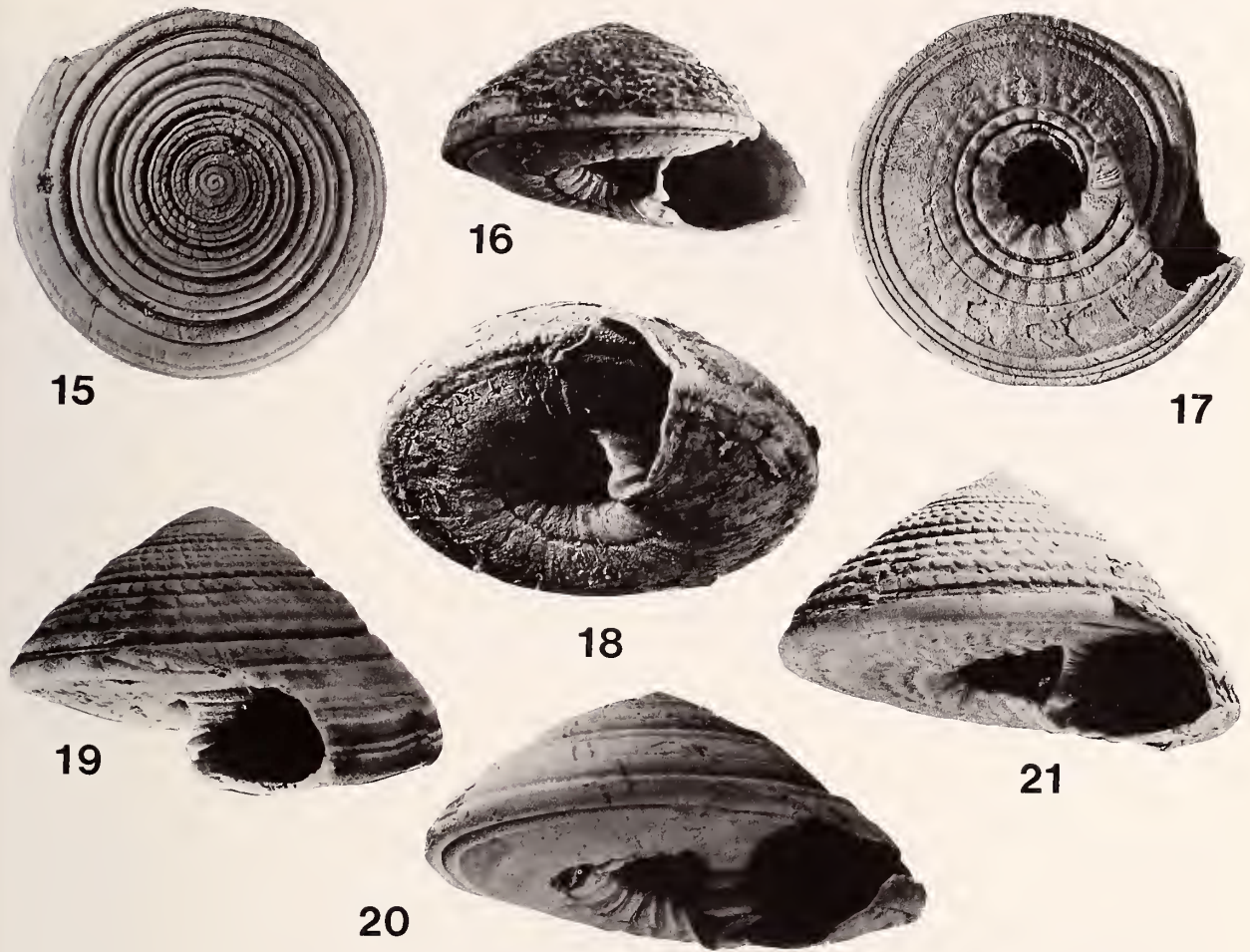
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Explanation of Figures 15 to 21

Figures 15, 16, 18, and 20. *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

Figure 15. PRI 20444 (= *A. sexlinearis haughti* Marks, 1951). Middle Miocene, Daule Formation, Ecuador. Dorsal view. Note presence of only three dorsal grooves on younger whorls. ($\times 1.46$).

Figure 16. LACM 66-198a. Recent, 93 m, off Cabo Pasado, Ecuador. Lateral view of columella showing position of principal adapical groove and weaker grooves abapically on the columellar lip. ($\times 1.45$).

Figure 18. LACM 66-198a. Oblique apertural view of columella. ($\times 1.45$).

Figure 20. USNM 562636. Miocene, Panama. Oblique apertural view of columella showing position of adapical groove and absence of pleating on columellar lip. ($\times 1.75$).

Figures 17, 19, and 21. *Architectonica (Architectonica) nobilis* Röding, 1798.

Figure 17. OSU 36794. Late Pleistocene, Lobitos Tablazo, northwestern Peru. Ventral view showing two strong grooves bordering the umbilicus. ($\times 1.75$).

Figure 19. OSU 36793. Recent, northwestern Peru. Apertural view showing pleated columellar lip.

Figure 21. LACM AHF-93839. Recent, Costa Rica. Apertural view showing position of columellar adapical groove and pleated columellar lip. ($\times 1.81$).

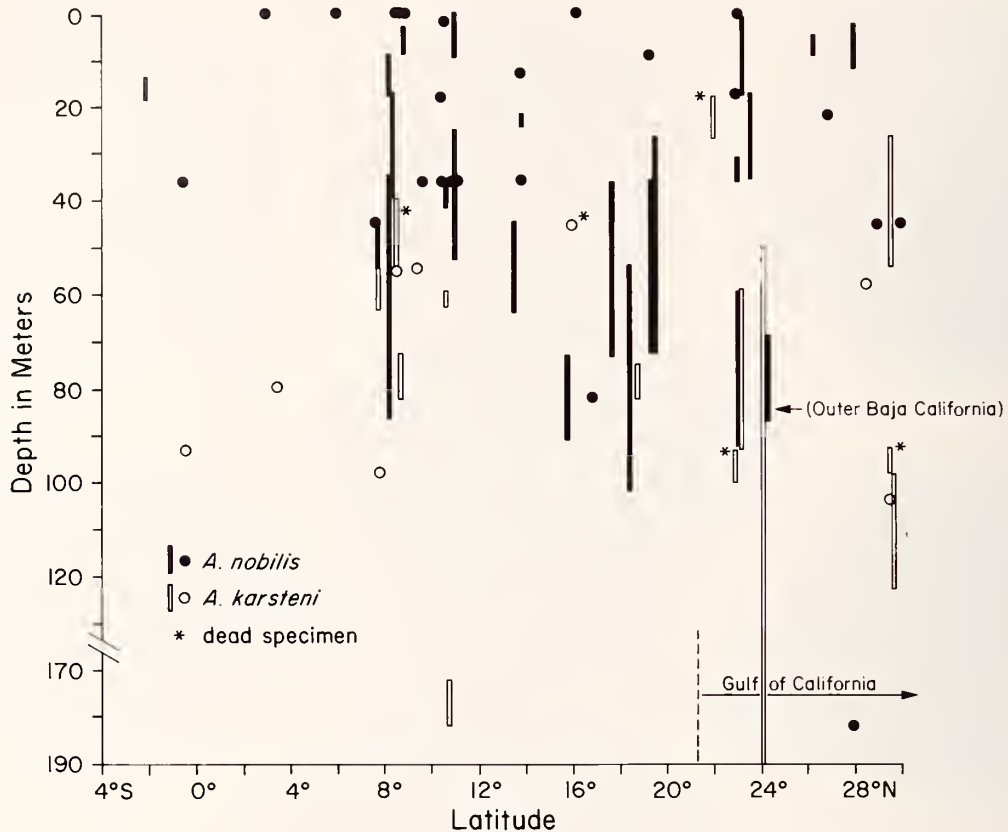


Figure 22

Latitudinal and bathymetric distribution of Recent *Architectonica* (*Architectonica*) *karsteni* (Rutsch). Data from collections of LACM; material collected by R/V *Anton Bruun* and other vessels.

bilicus. Thus, Toula's specimen is properly referred to *Architectonica nobilis*. TRECHMANN (1935) was correct in not assigning his Caribbean specimen to *A. nobilis*; when referring it to *S. gatunense*, he probably was unaware of RUTSCH's (1934) year-old description of *A. karsteni*.

As noted by RUTSCH (1934), *Architectonica karsteni* bears a strong resemblance to European Miocene species of the same subgenus, particularly *A. grateloupi* (d'Orbigny, 1852) (COSSMANN, 1915:164, pl. 6, figs. 40, 41, 42), *A. carocollatum* (Lamarck, 1822), and varieties of the latter (SACCO, 1892:40-41, pl. 1, fig. 35; STRAUZ, 1966: 115-116, pl. 52, figs. 5, 7-10). *Architectonica grateloupi* is less granulose than Recent *A. karsteni* but no less granulose than many fossil *A. karsteni*. Four dorsal cords are present on all whorls, as in Recent *A. karsteni*. The umbilicus is somewhat wider than in any *A. karsteni*. *Architectonica grateloupi* typically has not one, but two ventral spiral threads adjacent to the dorsal peripheral cord.

Architectonica carocollatum and *A. carocollatum* var. *palatinum* (STRAUSZ, 1966) are also less granulose than Recent *A. karsteni*. Dorsal grooves are variably developed. On the typical form of *A. carocollatum* only two of four grooves are carried forward to the penultimate and ultimate whorls. On the "*palatinum*" form, never more than two dorsal grooves are present on any whorl.

Considering the specificity of the characters pertaining to *Architectonica karsteni* in Recent populations and the rarity of gradations in character with *A. nobilis*, the persistence of these characters through 20 million years, the widespread geographic range of the "*karsteni*" form, past and present, and the ecological arguments presented below, it is concluded that *A. (A.) nobilis karsteni* should be elevated to specific status.

Despite some morphological overlap between Recent *Architectonica karsteni* and *A. nobilis*, there is no reason that *A. karsteni* must be considered a New World Neo-

Table 1

Dimensions of selected *Architectonica* specimens, including specimens of *A. karsteni* illustrated in this paper.

Specimen	Diameter (mm)	Height (mm)	H/D	Umbilical width (mm)	UW/D
<i>Architectonica karsteni</i>					
LACM 66-198a	33.5	21.4	0.64	12.6	0.38
LACM 66-198b	28.5	16.8	0.59	9.7	0.34
LACM 66-198c	28.0	15.6	0.56	10.0	0.36
LACM 66-198d	27.8	16.0	0.58	9.7	0.35
OSU 36792	27	?	—	11.2	0.40
USNM 562636	37	19	0.5	14	0.4
SGOP 13122	24.8	14.1	0.57	9.3	0.37
PRI 20443	19.9	12.5	0.63	6.9	0.35
PRI 20444	35.2	23.7	0.67	13.3	0.38
<i>Architectonica nobilis</i>					
AHF 939-39	38.2	24.1	0.63	14.9	0.39
OSU 36793	37.0	23.2	0.63	14.9	0.39
OSU 36794	31.0	16.4	0.53	10.9	0.35

gene descendant of *A. nobilis*, given the ubiquity of forms very similar to *A. karsteni* throughout the Miocene of Europe.

ECOLOGICAL CONSIDERATIONS

Most Recent specimens of *Architectonica karsteni* in the LACM collection were recovered from depths in excess of 50 m, whereas *A. nobilis* was usually found at lesser depths (Figure 22). Only along the narrow continental shelf between 16 and 24°N was *A. nobilis* common at depths greater than 50 m.

Most fossil specimens of *Architectonica karsteni* were probably deposited in an offshore setting (Table 2). Fossil *A. nobilis* occur in the same strata as *A. karsteni*, as well as in adjacent strata. There is no evidence that these occurrences in other strata are from solely nearshore sediments. Thus, the apparent modern segregation of the two species by water depth cannot be demonstrated for the fossil record. Nonetheless, there is little basis for believing that *A. karsteni* was ever a regular inhabitant of very shallow water.

The 50-m break in the Recent distribution of the two

Table 2

Sedimentological information pertaining to Neogene and Recent occurrences of *Architectonica* (*Architectonica*) *karsteni* (Rutsch).

Locality	Formation	Sedimentology	Age	Author
Punta Gavilan, n. Venezuela	"Cantaure" Fm.	Glauconite, limonitic sandy limestone	Miocene	RUTSCH, 1934
Paraguana Peninsula, n. Venezuela	"Cantaure" Fm.	60% clay; thin-bedded sandstone; thin-bedded limestone; 30 m above bedrock	middle Miocene	JUNG, 1965
Carriacou, Grenadine Islands	Grand Bay Fm.	Ashy shale, fine agglomerates; hermatypic and ahermatypic corals	middle Miocene	TRECHMANN, 1935; JUNG, 1971
Carriacou, Grenadine Islands	Kendace Fm.	Calcareous marls	late early Miocene	JUNG, 1971
Panama	La Boca Fm.	Silty or tuffaceous mudstone; minor conglomerate; coralline limestone	early Miocene	WOODRING, 1973
Panama	Chagras Fm.	Massive fine sandstone and siltstone; overlies barnacle coquina	late Miocene-early Pliocene	WOODRING, 1959
Daule Basin, Ecuador	Daule Fm.	Blue siltstone	middle Miocene	MARKS, 1951
Punta Perro, c. Chile	La Navidad Fm.	Coarse quartz sandstone	early-middle Miocene	FRASSINETTI & COVACEVICH, 1981
Tuxtepec, Mexico	—	Poorly consolidated sands	Pliocene	BOSE, 1906
Cabo Blanco, Peru	Mancora Tablazo beds	Calcareous, gravelly sandstone	late Pliocene-early Pleistocene	This paper
Ecuador to Gulf of California; Baja California Sur	—	Gravel; mud; fine sand; shells	Recent	This paper

Architectonica species in the eastern tropical Pacific Ocean is approximately coincident with the lower boundary of the permanent oceanic thermocline (e.g., PATZERT, 1978). Water temperatures immediately beneath the thermocline fluctuate seasonally but are generally several Centigrade degrees cooler than surface waters. Given that the isotherms at 50–100 m (within the depth range of *A. karsteni*) extend several latitudinal degrees beyond the poleward limits of the geographic range of *A. karsteni*, it would seem that this species is not making full use of its thermally defined habitat. Hence, geographic and bathymetric restraints on its distribution cannot be principally thermal. Nor does the restraint appear to be sedimentological, as live specimens of *A. karsteni* were dredged from all types of substrate. Factors not considered here, including competition, seasonal temperature changes interacting with the life history of the species, and circulation patterns, may exert more control on the distribution of this species.

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LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. 2nd edition. Van Nostrand Reinhold Co.: New York. 663 pp.
- BOSE, E. 1906. Sobre algunas faunas terciarias de México. Instit. Geol. de México Bol. 22:1–96.
- BOSWORTH, T. O. 1922. Geology of the Tertiary and Quaternary periods in the northwestern part of Peru. Macmillan and Co., Ltd.: London. 434 pp.
- COSSMANN, M. 1915. Essais de paléoconchologie comparée. Vol. 10. Paris.
- DEVRIES, T. J. 1982. Nearshore depositional sequences of the Peruvian Mancora Tablazo: prelude to Pleistocene biogeographic analysis. Geol. Soc. Amer. Abstr. with Progr. 14(7): 474.
- D'ORBIGNY, A. 1852. Prodrome de paléontologie stratigraphique universelle. Vol. 3. V. Masson: Paris.
- FRASSINETTI, D. & V. COVACEVICH. 1981. Architectonidae en la formación Navidad, Mioceno, Chile central, parte 2: *Architectonica* (*Architectonica*) *nobilis karsteni* Rutsch, 1934. Mus. Nac. Hist. Nat. Bol. 38:147–154.
- GARRARD, T. A. 1977. A revision of Australian Architectonicidae (Gastropoda: Mollusca). Records of the Australian Museum 31(13):506–584.
- GRAY, J. E. 1847. A list of the genera of recent Mollusca, their synonyma and types. Proc. Zool. Soc. Lond. 15:129–219.
- GRAY, M. E. 1850. Figures of molluscan animals. Vol. 4. 124 pp. London.
- JUNG, P. 1965. Miocene Mollusca from the Paraguana Peninsula, Venezuela. Bull. Amer. Paleont. 49(223):385–652.
- JUNG, P. 1971. Fossil mollusks from Carriacou, West Indies. Bull. Amer. Paleont. 61(269):147–262.
- KEEN, A. M. 1971. Sea shells of tropical west America. 2nd edition. Stanford University Press: Stanford, California. 1064 pp.
- LAMARCK, J. B. 1822. Histoire naturelle des animaux sans vertébrés. Vol. 7. Paris. 711 pp.
- LINNÉ, C. 1758. Systema naturae. 10 ed., reformata 1. Stockholm. 824 pp.
- MARKS, J. G. 1951. Miocene stratigraphy and paleontology of southwestern Ecuador. Bull. Amer. Paleont. 33(139):271–432.
- PATZERT, W. C. 1978. El Niño watch atlas. Scripps Instit. Oceanogr. Ref. Ser. No. 78-7. 322 pp.
- RÖDING, P. F. 1798. Museum Boltenianum . . . : pars secunda continens Conchylia . . . J. C. Trappii: Hamburg. 109 pp.
- RUTSCH, R. 1934. Die Gastropoden aus dem Neogen der Punta Gavilan in Nord-Venezuela. Schweizer. Paläont. Gesell. Abh. 54(3):1–88.
- SACCO, F. 1892. I molluschi dei terreni terziarii del Piemonte e della Liguria. Musei di Zool. ed Anat. Comp. della Reale Univers. di Torino Boll. 7(121):51–57.
- STRAUSZ, L. 1966. Die Miozän-Mediterranen Gastropoden Ungarns. Akademiai Kiado: Budapest. 535 pp.
- TOULA, F. 1908. Eine jungtertiäre Fauna von Gatun am Panama-Kanal. Jahrb. K.K. Geol. Reichsanstalt. 58(1908):673–760.
- TRECHMANN, C. T. 1935. The geology and fossils of Carriacou, West Indies. Geol. Mag. 72(12):529–555.
- WOODRING, W. P. 1959. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Vermetidae to Thaididae). U.S. Geol. Surv. Prof. Paper 306-B:147–239.
- WOODRING, W. P. 1973. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Additions to gastropods, scaphopods, pelecypods: Nuculidae to Malleidae). U.S. Geol. Surv. Prof. Paper 306-E:453–539.